

TAXONOMIC TREATMENT OF THE  
*CHAETOMORPHA* AND *RHIZOCLONIUM*  
SPECIES (CLADOPHORALES; CHLOROPHYTA)  
IN NEW ENGLAND<sup>1</sup>

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ABSTRACT

A key to the species of *Chaetomorpha* and *Rhizoclonium* found in New England is presented along with a description and review of each species' ecology, distribution, and taxonomic history. *Chaetomorpha picquotiana* is shown to be an earlier name for *C. atrovirens*, and discussions concerning the generic placement of *Chaetomorpha cannabina* and the separation of the genera *Chaetomorpha* and *Rhizoclonium* are presented.

The genera *Chaetomorpha* Kützing (1845) and *Rhizoclonium* Kützing (1843) have posed numerous taxonomic problems for phycologists. The reasons for these problems appear multifold. A general lack of understanding of the phenotypic variability of species at the time of their description, a small number of characters of taxonomic significance, and varied interpretations of morphological circumscription have resulted in the recognition of ill-defined species within these genera.

In attempting to resolve this confusion, it is essential to determine the reliability of as many characters as possible. Unfortunately a number of characters used in the past are dependent on plant maturity (number of nuclei per cell, cell wall thickness and stratification, pyrenoid number, reproductive patterns) and on environmental conditions (color, state of attachment, rhizoid number and complexity). The suitability of application of such characters should, therefore, be evaluated on a species-by-species basis. At present, evaluation of morphological variability remains the major basis for species circumscription.

A previous report (Blair, et al., 1982) described the electrophoretic and morphological patterns and specific separation of

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*Chaetomorpha linum* (Müll.) Küt., *C. aerēa* (Dillw.) Küt., *C. picquotiana* Montagne ex Kützing (as *C. atrovirens* Taylor) and *C. melagonium* (Web. et Mohr) Küt. based on a morphological and biochemical analysis of the species *Chaetomorpha* and *Rhizoclonium* in New England (Blair, 1978). The present report summarizes the morphological findings of the latter report through presentation of artificial keys and descriptions of the species, and reviews the ecology, distribution, and taxonomic history of each species. Acronyms for herbaria follow those of Holmgren and Keuken (1974).

KEY TO THE SPECIES OF CHAETOMORPHA AND  
RHIZOCLONIUM IN NEW ENGLAND

1. Filaments uniseriate, attached by a single basal cell, or unattached and greater than 75  $\mu\text{m}$  diam. . . . .  
 . . . . . *Chaetomorpha* p. 176.  
 1. Filaments unattached, with or without rhizoids, and less than 75  $\mu\text{m}$  diam. . . . .  
 . . . . . *Rhizoclonium* p. 197.

CHAETOMORPHA

**Chaetomorpha** Kützing (1845) Phyco.  
Germ p. 203 (nom. cons.)

TYPE: *Chaetomorpha melagonium* (Web. & Mohr) Kützing.  
(1845) Phyco. Germ. p. 204

Type locality; North Sea

*Chloronitum* Gail. et Levrault (1828) Dict. Sci. Not. Vol. LIII p. 389-390.

*Spongopsis* Kützing (1843) Phyco. Gen. p. 261.

*Aplonema* Hassel (1845) Brit. Fresh. Alg. p. 213.

The genus *Chaetomorpha* contains species of uniseriate unbranched filaments with multinucleated cells, and a single reticulate parietal chloroplast containing numerous pyrenoids. Attachment is by a discoid holdfast cell (basal cell) which may produce "haptera-like" projections capable of "budding" off new plants. All of the species have an attached stage at some period in their life history. Some species become detached and remain in drift for the major part of their life span. Unattached species often become entangled among coarse algae and are capable of forming extensive masses. All of the species investigated thus far exhibit an isomorphic alter-



nation of generations by isogamous biflagellate gametes and quadri-flagellate zoospores. Some species may recycle the same generation via bi- or quadriflagellate zoospores.

### Taxonomic History

The genus *Chaetomorpha*, established by Kützing in 1845, was predated by Kützing's *Spongopsis* (Kützing, 1843) and Gaillon's (1828) *Chloronitum*. Due to the general acceptance of the name *Chaetomorpha*, Silva (1950) proposed that it be conserved. The proposal was accepted and listed under "Generica Conservada" in the International Code of Botanical Nomenclature (Stafleu, 1956).

#### KEY TO THE NEW ENGLAND SPECIES OF CHAETOMORPHA

1. Filaments attached by a basal cell . . . . . 2.
  2. Filaments less than 75  $\mu\text{m}$  diam., epiphytic on coarse algae . . . . . *C. minima* p. 195.
  2. Filaments greater than 75  $\mu\text{m}$  diam. . . . . 3.
    3. Filaments erect, straight, 350 to 850 (<1000)  $\mu\text{m}$  wide, with basal cell length/width ratio (LWR) of 10 to 12, plants of sublittoral or low intertidal pools . . . . . *C. melagonium* p. 190.
    3. Filaments less than 350  $\mu\text{m}$  wide, curled or having basal cell LWR of less than 8 . . . . . 4.
      4. Basal cell much longer than cells of the upper portion of the filament . . . . . 5.
        5. Filaments curled, cells 175–450  $\mu\text{m}$  diam., basal cell LWR less than 5, plants of mid-littoral or sublittoral region . . . . . *C. linum* p. 178.
        5. Filaments straight, cells 125–400  $\mu\text{m}$  diam., basal cell LWR to 10, plants of mid and high littoral pools . . . . . *C. aerea* p. 187.
      4. Basal cell not longer than cells of the upper filament . . . . . 6.
        6. Cells 200–400  $\mu\text{m}$  diam., curled, mean cell LWR 2.0–5.0 . . . . . *C. piquotiana* p. 181
        6. Cells 75–150  $\mu\text{m}$  diam., curled or straight, mean cell LWR 0.75–3.0 . . . . . *C. brachygona* p. 192.
1. Filaments unattached, though often intricately entangled among coarse algae . . . . . 7.



7. Cells 75–150  $\mu\text{m}$  diam., mean cell LWR 0.75–3.0 .....  
 ..... *C. brachygona* p. 192.
7. Cells 150–450  $\mu\text{m}$  diam., mean cell LWR 0.75–1.5 or  
 2.0–5.0 ..... 8.
8. Filaments curled, cells 150–450  $\mu\text{m}$  diam., usually light  
 green, mean cell LWR 0.75–1.5 ..... *C. linum* p. 178.
8. Filaments curled, cells 200–400  $\mu\text{m}$  diam., usually dark  
 green, mean cell LWR 2.0–5.0... *C. piquotiana* p. 181.

**Chaetomorpha linum** (Müller) Kützing (1845) *Phyco. Germ.* p. 204  
 Basionym: *Conferva linum* Müller (1778) *Flora Danica*.  
 5(13)

TYPE: *Conferva linum* Müller (1778) *Flora Danica*. 5(13) t.  
 771 f. 2

Type locality: Nakskov Fjord and Rodby Fjord, Denmark.

*Conferva capillaris* L. 1753. *Sps. Plant.* 2:1166.

*Chaetomorpha chlorotica* (Mont.) Kütz. 1849. *Sps. Alg.*, p. 377; 1853. *Tab. Phyc.*, III, t. 54, f. 1

*Chaetomorpha brachyartha* Kütz. 1853. *Tab. Phyc.* t. 53, f. 4.

*Conferva brachyartha* Kütz. 1843. *Phyco. Gen.* p. 206.

*Conferva capillaris* Dillw. 1806. *Brit. Conf.* t. 9, p. 46.

*Chaetomorpha dalmatic* Küt. 1845. *Phyco. Germ.* t. 203; 1853. *Tab. Phyc.* III t.  
 57, f. 1.

*Chaetomorpha setacea* (Ag.) Küt. 1849. *Sps. Alg.* p. 378; 1853. *Tab. Phyc.* III t.  
 4, f. 1.

*Conferva setacea* C. Ag. 1824. *Sys. Alg.* p. 98.

*Chaetomorpha urbica* (Zand.) Küt. 1847. *Bot. Zietg.* V:168; 1853. *Tab. Phyc.*  
 III t. 54, f. 3.

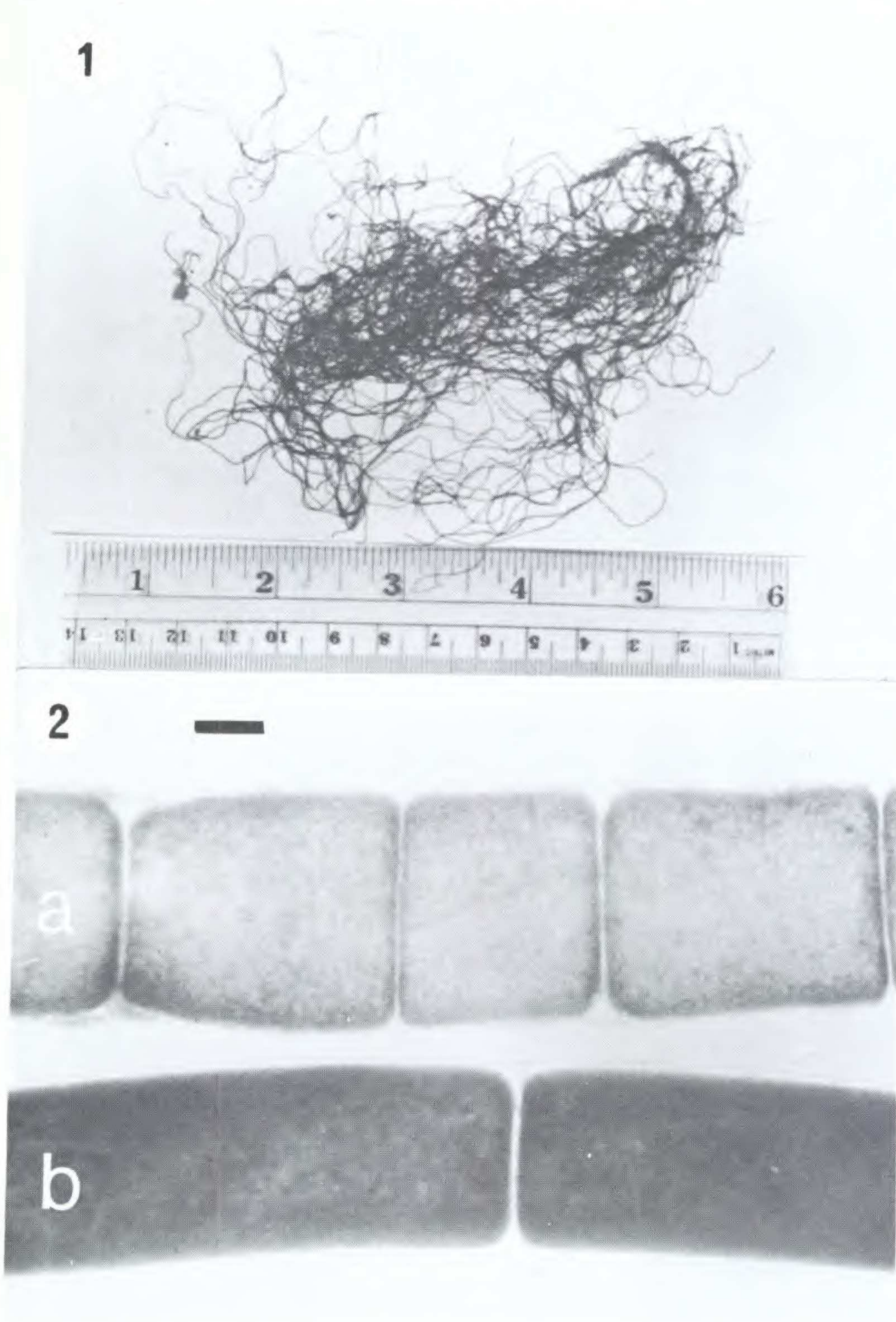
*Chaetomorpha aerea* (Dillw.) Küt. f. *linum* (Müll.) Collins 1909. *Grn. Agl. of*  
*N. Amer.* p. 325.

The plants (Fig. 1) are usually found entangled and unattached among coarse algae, rarely found attached (initially) by a single basal cell. The plants are stiff, not collapsing on removal from water, the cells are cylindrical to barrel shaped with a diameter of 150–450  $\mu\text{m}$  and a LWR (length/width ratio) of 0.75 to 1.5 (Fig. 2a). The basal cell, when present, is 3 to 8 times longer than broad. Gametes are reported from April to August, zoospores from August to November (Taylor, 1957), though no fertile material was found in specimens examined.

#### Distribution and Ecology

The species shows a world-wide distribution, extending from





Figures 1 and 2. Fig. 1, Habit of *Chaetomorpha linum*. Fig. 2, comparative cell sizes of *C. linum* and *C. picquotiana*. 2a — *C. linum*, 2b — *C. picquotiana* (Scale = 100  $\mu$ m).



Panama to Labrador, South Africa to Norway, Australia to Japan and California to Alaska. In New Hampshire it occurs in coastal and estuarine areas with decreasing abundance in inner estuarine locales where salinities are less than 10 ppt. It grows within the littoral zone, entangled among coarse algae and in tide pools, as well as to -18 m below MLW. In estuarine tidal rapids this species may form extensive masses (skeins) up to 3 m in length and 0.5 m diam. Kornmann (1972) and Patel (1972) have induced sporulation and gametogenesis in culture but they give no records of in situ reproductive phenology.

#### Representative Specimens:

**Africa.** Comerunia Jungner, Wittrock & Nordstedt Algae Exsic. 1049 (UC). **Australia.** Coffin Bay: *Womersly A31820* (UC). **Bermuda.** Hamilton Harbor; *Collins s.n.* 5 March 1913 (UC). Faryland; *Collins 311* (FH). **Canada.** NEWFOUNDLAND: Alexander Bay, *Hooper & Roberge 10144* (NFLD); Placentia Bay, *Whittick & Hooper 8393* (NFLD). NOVA SCOTIA: Dunns Beach, *South and Whittick 6751* (NFLD). **Chile.** Valparaiso, Montinom, *Etchenerry s.n.*, 1951, (UC). **France.** Cherbourg: LeJolis, *Algeres Marines de Cherbourg 258* (UC). Banyuls, *Feldman 1726* (UC). **Holland.** Nievnedup, Weber-Von Bose, *Hauk et Richter Phyco. Univ. 125, & 468*, (UC). **India.** *Wright s.n.*, (FH). **Italy.** Isola di Caprera, *Levi-Monenas, Phyco. Italica 185* (UC). **Japan.** Enoshima, Kamara, K. 9 Alg. *Japanica Exsic. 93* (UC). **Panama.** Caledonia Harbor: *Taylor 39-183* (UC, FH). **Philippines.** Guanica Harbor: *Howe, N. Amer. Marine Algae 7035* (FH, UC). **Sweden.** Bhausia Maj: *Areschoug, Alg. Scand. Exsic. Fasc. secundus 134* (UC). **Tahiti.** Society Island: Tilden, *South Pacific Algae 21* (UC). **United States.** ALASKA: Tangas Is., *Lichentater 1887* (FH). CALIFORNIA: Santa Clara Co., San Martin Is., *Howe 201* (UC). MAINE: York Co., Kittery, Malaga Is., *Mathieson s.n.*, 16 April 1976 (NHA). Seapoint, *Blair s.n.*, 2 October 1977 (NHA). MASSACHUSETTS: Barnstable Co., Woods Hole, *Doty 6722* (FH). Buzzard's Bay, *Taylor s.n.*, 2 August 1944 (NFLD). Gloucester, *Farlow Algae Exsic. Am.-Bor. 175* (FH). Salem, *Hauk, Collins Et Richter Phyco. Univ. 469* (FH). NEW HAMPSHIRE: Rockingham Co., Dover, *Mathieson s.n.*, 21 October 1977 (NHA). *Mathieson s.n.*, 3 August 1976 (NHA). Newington, *Conway et. al. s.n.*, 6 July 1966 (NHA). Portsmouth, *Conway & Hehre s.n.*, 20 April 1966 (NHA). Durham, Adam's Point, *Mathieson s.n.*, 30 December 1973 (NHA). NEW JERSEY: Monmouth Co., *Maul s.n.*, 17 October 1956 (UC). OREGON: Coos Co., *Chadwick 907* (UC). RHODE ISLAND: Newport Co., Newport, *Clark s.n.*, July 1890 (FH).

**Yucatan:** Campeche Bank, *Connover & Perkins s.n.*, 15 July 1960 (NHA).

#### Taxonomic History

*Chaetomorpha linum* was described in *Species Plantarum* (Linnaeus, 1753) under the name *Conferva capillaris*. The filaments were described as being simple, with joints alternately compressing on drying. Müller's (1778) original description of *Conferva linum* was very similar to *C. capillaris* L. Subsequently, Roth (1797) gave



separate descriptions of *C. linum* and *C. capillaris*. It is apparent that the name *C. linum* has been maintained due to its more detailed description. Børgesen (1925) noted the nomenclatural confusion between *Conferva capillaris* and *C. linum* and proposed the acceptance of *C. linum* over *C. capillaris* due to its long usage and entrenchment. However, the International Code of Botanical Nomenclature (Stafleu, 1978) has no provision for the conservation of species names.

It should be noted that the transfer of *Conferva capillaris* L. to *Chaetomorpha* would create a homonym with *C. capillaris* (Kützing) Børgesen, contrary to Article 55, of the International Code of Botanical Nomenclature (Stafleu, 1978). Thus, the next validly published name, *Conferva linum* Müller, may be applied to the taxon. *Conferva linum* Müller was transferred to *Chaetomorpha* by Kützing (1849); as a result *Chaetomorpha linum* (Müller) Kützing is the correct name, with *C. capillaris* L. being placed into synonymy. The confusion between *C. linum* and *C. aerea* is discussed in the taxonomic history section under *C. aerea*.

***Chaetomorpha picquotiana*** Montagne ex Kützing 1849. Species  
Algarum p. 379

Basionym: *Conferva picquotiana* Montagne. 1849. Ann.  
Sci. Nat. 3d Ser. 11: 66.

LECTOTYPE?: *Conferva picquotiana* Lamare-Picquot s.n.  
(PC) in (FH)

Type locality: Labrador

*Chaetomorpha melagonium* f. *typica* Kjellman sensu Collins 1909. Green Alg.  
of N. America. p. 323.

*Chaetomorpha atrovirens* Taylor. 1937. Pap. Mich. Acad. Sci. Arts. Lett. 22:  
227-8.

The species forms entangled masses in littoral pools as well as among coarse algae in the littoral and sublittoral zones (Fig. 3). The cells range from 225–400  $\mu\text{m}$  in diameter with LWR's of 2–8 (Fig. 2b). Juvenile attached filaments have an attenuated basal cell (Fig. 4) which is similar in diameter to the upper cells of the filament. The discoid holdfast cell may form non-septate rhizoidal projections. The species is distinguished from *Chaetomorpha linum* by its larger LWR, *C. picquotiana* being greater than 2.0 while *C. linum* is less than 1.5 (Blair, et al., 1982). The plant reproduces by vegetative



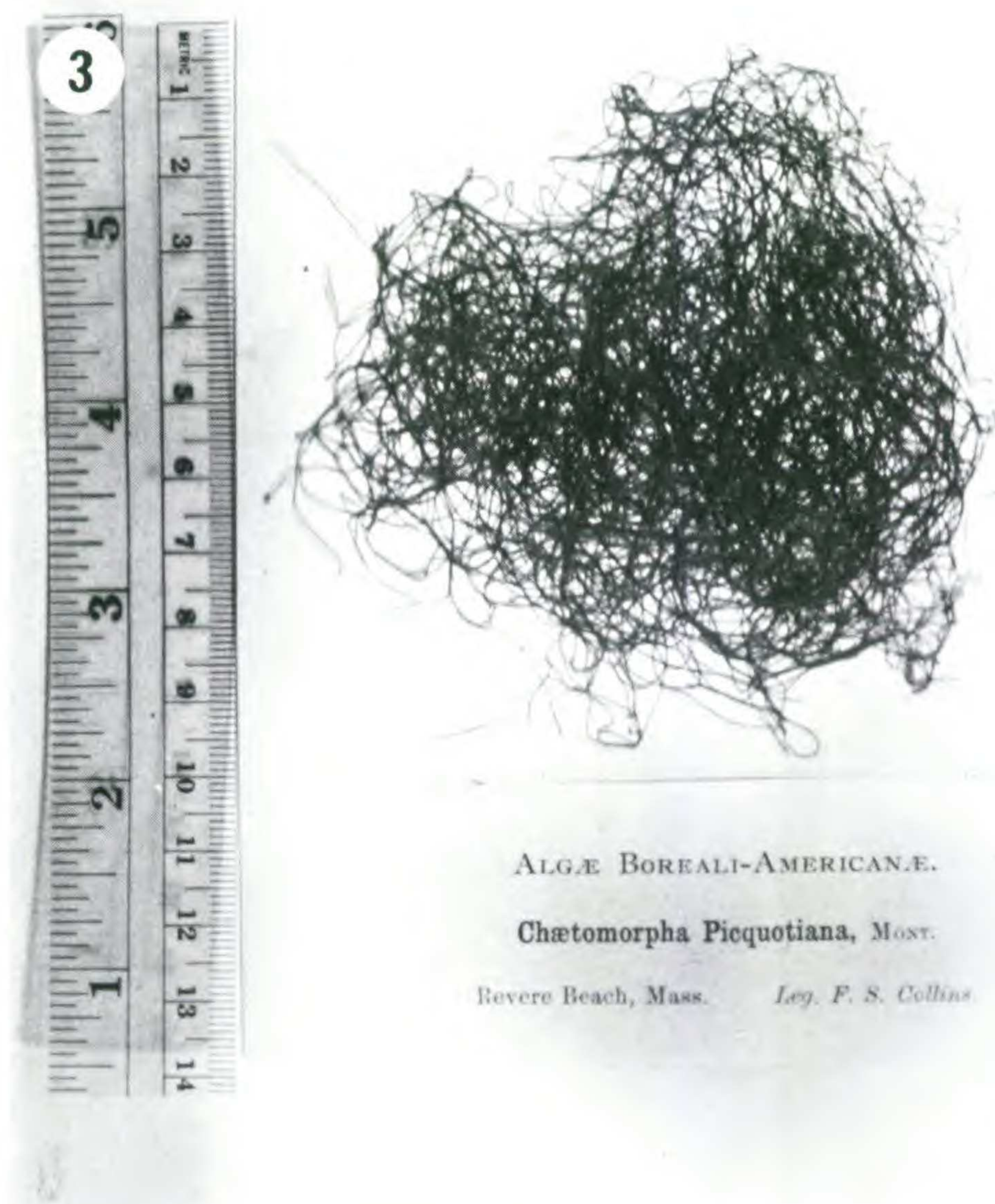


Figure 3. Habit of *Chaetomorpha picquotiana*.

propagation (i.e., fragmentation). An isomorphic alternation of generations is assumed to occur.

#### Distribution and Ecology

*Chaetomorpha picquotiana* has its major center of distribution in northern North America, north of Long Island on the east coast, and from Oregon northwards on the west coast. However, a few records of *C. picquotiana* have been confirmed from Florida and Bermuda. The species distribution is very similar to that of *C. melagonium* with which it may be closely related (Blair, et al., 1982).



*Chaetomorpha picquotiana* shows a broad distribution within the Great Bay estuary, New Hampshire, except at the headwaters of riverine habitats where salinities are less than 10 ppt.

#### Representative specimens:

**Bermuda.** Hamilton Islands: *Bernatowicz* 49-624 (UC), *Hamilton GRO* 2807 (NFLD). **Canada.** BRITISH COLUMBIA, Henderson Point, *Hooper s.n.*, 2 January 1971 (NFLD). LABRADOR. *Lamare-Picquot s.n.* (PC) in (FH). NEWFOUNDLAND. Little Bay Est., *South, Whittick* 413 (NFLD); Salmonier, *Mathieson* 9d (NFLD); Placentia Bay, *Hooper & Reddin* 12495 (NFLD). NOVA SCOTIA. Muder Island, *Hooper* 15264 (NFLD). PRINCE EDWARD ISLAND. *Macon s.n.*, 29 June 1888 (FH).

**United States.** ALASKA. Unalaska, *Womersley* 1848 (FH). FLORIDA. Monroe Co., Key West, *Curtis s.n.*, August 1895 (FH). MAINE. Cumberland Co., South Harpswell, *Tyler & Brannigan s.n.*, 4 March 1966 (NHA). Knox Co., Rockland, *Clarke s.n.*, 3 December 1895 (NFLD). York Co., Kittery, *Mathieson s.n.*, 16 June 1966 (NHA), *Blair s.n.*, 6 December 1977 (NHA). MASSACHUSETTS. Barnstable Co., Great Brewster Is., *Hutchinson s.n.*, 20 October 1971 (NHA). Salem, *Femino s.n.*, 4 August 1966 (NHA). Gloucester, *Farlow s.n.*, September 1878 (FH). Revere Beach, *Collins s.n.*, 12 April 1884 (FH). Swampscott, *Collins s.n.*, (FH). NEW HAMPSHIRE. Rockingham Co., Hampton, *Mathieson s.n.*, 19 April 1966 (NHA). Seabrook, *Hutchinson* B431 (NHA), *Searles s.n.*, 7 March 1966 (NHA). Portsmouth, *Cheney & Kilar s.n.*, 27 February 1976 (NHA). Newcastle, *Voorhees & Mathieson s.n.*, 24 July 1976 (NHA). Strafford Co., Dover, *Mathieson s.n.*, 20 April 1977 (NHA). RHODE ISLAND. Newport Co., *Kingston s.n.*, (NHA).

#### Taxonomic History

The species was described by Montagne (1849) as *Conferva picquotiana*. Kützing (1849) published *Chaetomorpha picquotiana* attributing it to Montagne, "in litt.". Therefore as suggested by P. C. Silva (pers. comm.) the authorization of *Chaetomorpha picquotiana* is best attributed to Montagne ex Kützing. Much of the confusion concerning this taxon's proper specific designation centered around the fact that the species was described as being attached. This, in combination with the length of the cells, has led authors to speculate that *C. picquotiana* and *C. melagonium* were conspecific, and that a long celled unattached species, *C. atrovirens* Taylor (1937) was simply a detached phase of the attached plant. Harvey (1857) was the first to express an opinion on the relationship between *C. picquotiana* and *C. melagonium*. He compared Montagne's material with *Chaetomorpha melagonium* and concluded the two were separate species but noted that *C. picquotiana* "is nearly related to *C. melagonium*, but of larger dimensions and with much longer articulations". It should be noted that Harvey was





Figure 4. Basal holdfast cell of a *C. picquotiana* filament (Scale = 100  $\mu\text{m}$ ).



applying the name *C. picquotiana* to the detached, entangled entity (*C. atrovirens* sensu Taylor) and had not found the species attached. Farlow (1881), also referring to unattached material, stated that it was "probable" that "it is merely an advanced stage" of *C. melagonium* that had broken off. Kjellman (1889) placed *C. picquotiana* under *Chaetomorpha melagonium* f. *typica* Kjellm. Kjellman cited Kützing's illustration of *C. picquotiana* (Kützing, 1853), Weber and Mohr's description of *C. melagonium* (Weber & Mohr, 1804) and Wittrock and Nordstedt's specimen of *C. melagonium* (Witt. and Nords. Alg. Exsicc. 1877-87 #415). As no explanation of the synonymy was given it may only be speculated that similarities in the original descriptions led Kjellman to place *C. picquotiana* into synonymy. Unfortunately, Kjellman did not state whether the *C. picquotiana* of Harvey and Farlow (unattached material) should be included with it. Collins (1909) carried forth the classification of Kjellman and the interpretation of Harvey and Farlow, referring to the unattached material as *C. melagonium* f. *typica*. Collins noted that the unattached material had previously been known as *C. picquotiana* "but is now pretty generally recognized as a form of the present species." Setchell and Gardner (1920) discussed the varied usage of *C. picquotiana* and *C. melagonium* f. *typica*. They felt that due to the similarity of the original descriptions of the plants, that Kjellman's placement of *C. picquotiana* under *C. melagonium* may be proper. Further, they questioned whether unattached material found in New England had been properly designated as *C. picquotiana*, for if, as Harvey and Farlow believed, it was simply a detached phase of the attached material, then such a "phase" would be present on the Pacific Coast in the regions where *C. melagonium* occurs. The apparent absence of the phase on the northwest coast led them to discount the application of *C. picquotiana* to the unattached material in New England. Taylor (1937) proposed the name *Chaetomorpha atrovirens* for the unattached, entangled New England species. Taylor discounted the previous designations of the taxon as *C. melagonium* f. *typica* on the basis of a lack of "any convincing demonstration" of a relationship between *C. melagonium* and the unattached plant, and cited the objections of Setchell and Gardner to the use of *C. picquotiana*. It should be noted that of the above authors only Harvey examined original material of *C. picquotiana*.

Thus, *Chaetomorpha picquotiana* has remained in synonymy



under *Chaetomorpha melagonium* and the unattached material has been referred to as *C. atrovirens*. Through the courtesy of the National Museum of Natural History, Paris (PC) and the Farlow Herbarium of Harvard University, Cambridge (FH), original specimens of *Conferva picquotiana* from Montagne's herbarium were examined. The specimens bore little resemblance to *C. melagonium*. The cells of the *C. picquotiana* filaments ranged in length from 609 to 1551  $\mu\text{m}$  (mean = 963) and in width from 250 to 325  $\mu\text{m}$  (mean = 284.5). The length/width ratios ranged between 2.1 and 5.4 (mean = 3.4). The above dimensions are well within the cell ranges shown by Blair, et al. (1982) for populations of *C. atrovirens*. The cells of *C. picquotiana* did not show an increase in length toward either end of the filament. The filaments showed much greater length/width ratios in the upper portions of the filament and longer and shorter cells were apparently randomly situated within the filament, as compared to a decrease in LWRs seen in the upper portion of *C. melagonium* filaments. The overall habit of the *C. picquotiana* specimens was indistinguishable from samples of *C. atrovirens* distributed in Collins' Phyco. Bor.-Amer. and those on deposit in the Herbarium of the University of Michigan, Ann Arbor (MICH) and in W. R. Taylor's herbarium.

As stated before, the apparent reason for indecision on the classification of this plant was the reference to the basal attachment in the original description. It should be noted that none of the original material examined, nor the illustrations (Kützing 1853; Harvey 1857), showed any holdfast or attachment cell. As seen in Fig. 4, the unattached New England material may initially be attached, by a modestly differentiated basal cell. The lack of an indication of attachment other than the basal cell itself means that if the lower portion of the holdfast cell were broken off during collection, all signs of attachment would be destroyed. This could account for the reference to basal attachment in the original description and absence of any signs of holdfasts on the original samples.

Thus, on the basis of the overall dissimilarity of *Chaetomorpha picquotiana* with *C. melagonium*, *C. picquotiana* should be removed from synonymy with *C. melagonium*. Further, due to the morphological inseparability of original specimens of *C. picquotiana* and *C. atrovirens* and for reasons stated above, it is apparent that *C. picquotiana* and *C. atrovirens* are conspecific. *Chaetomorpha picquo-*



*tiana* is the earlier name and *C. atrovirens* Taylor should be placed into synonymy under *C. picquotiana*.

***Chaetomorpha aerea*** (Dillwyn) Kützing. 1849. *Species Algarum* p. 379–380.

Basionym: *Conferva aerea* Dillwyn. 1806. *Syn. of Brit. Conf.*

TYPE: *Conferva aerea* Dillwyn. 1806. *Syn. of Brit. Conf.* Tab. 61.

Type Locality: Yarmouth Beach, England.

*Chaetomorpha princeps* Küt. 1849. *Sps. Alg.* P. 380.

*Conferva princeps* Küt. 1843. *Phyco Gen.* p. 206.

*Chaetomorpha variabilis* Küt. 1849. *Sps. Alg.* p. 378; 1853. *Tab. Phyc.* III t. 55.

*Conferva variabilis* Küt. 1843. *Phyco. Gen.* P. 260.

*Chaetomorpha dubyana* Küt. 1849. *Sps. Alg.* p. 378; 1853. *Tab. Phyc.* III t. 57 f. 3.

*Conferva dubyana* Küt. 1843. *Phyco. Gen.* p. 260.

*Chaetomorpha linum* (Müller) Küt. f. *aerea* Dillw. sensu Collins 1918. *Grn. Alg. of N. Amer. Sup.* p. 79; Farlow, 1881. *Mar. Alg. of New Eng. and Adj. Coast.* p. 46

*Chaetomorpha aerea* (Dillwyn) Küt. f. *aerea* (Dillw.) Collins. 1909. *Grn. Alg. of N. Amer.* p. 324.

*Chaetomorpha linum* (Müll.) Küt. sensu Abbot and Hollenberg. 1976. p. 101 (in part).

The species (Fig. 5) grows attached by a discoid basal cell and is often found growing in turf-like masses. Cell diameters range from 125–400  $\mu\text{m}$  (600  $\mu\text{m}$  when fertile), except for the basal cell, which is somewhat narrower and attenuated basipetally. The LWR of the upper cells is 1.5 to 2.5, while the basal cells range between 3 and 8 (Fig. 6).

#### Distribution and Ecology

The species has a world-wide distribution, from the Pacific and Atlantic coasts of the U.S.A., and from Canada, Norway, France, Spain, South Africa, Australia, the Philippines, Japan, and China. In New England, it grows in open coastal littoral pools within the mid and upper littoral zone. No estuarine records are known. *Chaetomorpha aerea* is found all year. It has an isomorphic alternation of generations (Hartman, 1929) and is reported to form zoospores in early summer (Taylor, 1957).





Figures 5 and 6. *Chaetomorpha aerea*. Fig. 5, habit of *C. aerea*. Fig. 6, basal region of filament with holdfast cells (Scale = 200  $\mu$ m).



## Representative specimens:

**Australia.** Rottrest Is., *Nash & Nash 41* (UC). Kangaroo Is., *Womersley s.n.*, April 1949 (UC). **Austria.** Flora Exsicc. Austro-Hungarian 1590 (FH). **Canada.** NEWFOUNDLAND: Bonne Bay, *Hooper & Roberge 8939* (NFLD). **Canary Islands.** Las Palmas, *Børgesen 4058* (UC). **Chile.** Chiloe, *Hieneck & Meerlagen 254* (UC). **China.** Fukien, *Chood A891* (UC); *Tsingyao 83* (UC). **Cuba.** Bahia Matanzos, *Dawson 7755* (UC). **France.** Bonflavor, *Thurst 156* (FH). Cherbourg, *Thurst 157* (FH). **Great Britain.** *Collins 86* (FH). **Italy.** Cagliori, *Canepa Erb. Criff Stal. Ser. II 778-779* (UC). Genova, *Canepa Erb. Criff Stal. Ser. II 361* (UC). **Jamaica.** Port Antonis, *Pease & Buttler s.n.*, July 1894 (FH). **Japan.** Tsugaru Strait, *Rosenbaum s.n.*, 30 July 1917 (UC). **Jugoslavia.** Trieste, Alg. Adriatacae Exsicc. 36-1911 (FH); *Hoeneck & Meerlagen 305* (UC). **Mexico.** Bihiak, *Dawson 1079* (UC). Punta Rosalia, *Dawson 2830* (UC). **New Zealand.** Bay of Islands, *Nash & Nash 347* (NFLD). **Norway.** Lille Svartskjar, Folsie, Witt. & Nord. Alg. Exsicc. 946 (UC). **Puerto Rico,** *Patillor, Alamodovar & Rolad 4218* (UC). **South Africa.** East Landon, *Niekirk 42* (UC). **Spain.** Borquera, *Sauvageau s.n.*, September 1896 (FH). **Sweden.** Bohuslan, *Kylin s.n.*, 8 July 1907 (UC).

**United States.** CALIFORNIA: Orange Co., Laguna Beach, *Mathieson s.n.*, 23 June 1969 (NHA); Monterey Co., Monterey Pen., *Mathieson s.n.*, 26 June 1960 (NHA), *Doty 4336* (FH). Pt. Fermin, Gardner Algae dist. from U. of California 37 (UC). San Diego Co., San Diego, *Collins, Holden & Setchell 76* (NHA); La Jolla, *Dawson 9566* (UC). MAINE: Hancock Co., Gouldsboro Bay, *Taylor s.n.*, 18 August 1960 (FH); Reid State Park, *Whittick & Hooper 6754* (FH). MASSACHUSETTS: Essex Co., Magnolia, *Clark s.n.*, 25 October 1889 (FH). NEW HAMPSHIRE: Rockingham Co., Seabrook, *Wells s.n.*, 21 September 1966 (NHA). Dover, *Mathieson s.n.*, 3 October 1977 (NHA). Newcastle, *Mathieson s.n.*, 20 June 1966 (NHA). Portsmouth, *Lamb A-99* (FH).

## Taxonomic History

*Chaetomorpha aerea* (Dillwyn) Kützing was initially described as *Conferva aerea* (Dillwyn, 1806). The species was described as basally attached in tufts and being as "brittle as *C. capillaris*" (= *C. linum*) "but not at all curled or entangled as that species."

The possible conspecific relationship between *Chaetomorpha linum* and *C. aerea* was first expressed by Rosenvinge (1893), by stating the belief that *C. linum* was a detached state of *C. aerea*. Subsequently, the two have been designated as forms of one species by some authors and as distinct species by others. For example, Collins (1909) formally designated *C. linum* as a form of *C. aerea* (*C. aerea* f. *linum*). He later (Collins, 1918) stated that *C. linum* had priority over *C. aerea* and classified the taxa *C. linum* f. *linum* and *C. linum* f. *aerea*, respectively. Christensen (1957) showed apparent transitional stages between attached (*C. aerea*) and detached (*C. linum*) entities and followed Collins' (1918) nomenclature. Price (1967) also favored a forma designation for the two taxa, and



expressed the opinion that no conclusive evidence had been shown for recognition at the specific rank. In contrast, Taylor recognized two distinct taxa (*C. aerea* and *C. linum*) but stated no justification. Patel's (1971a) cytological studies support Taylor's classification, reporting  $n = 18$  in *C. linum* and  $n = 12$  in *C. aerea*. Further evidence for their separation was given by Kornmann (1972), who showed that the taxa exhibited independent isomorphic alternation of generations. That is, *C. linum* showed a complete life history while *C. aerea* recycled itself by means of bi- or quadraflagellate zoospores. Most recently, biochemical information concerning genetic differences has been outlined by Blair et. al. (1982). Thus, evidence is present for the retention of two distinct taxa.

***Chaetomorpha melagonium*** (Weber et Mohr) Kützing 1845. Phyco. Germ. P. 204

Basionym: *Conferva melagonium* Weber et Mohr. 1804. Naturhistorische Reise durch einen Teil Schwedens. p. 149 t. 3, f. 2a & 2b.

TYPE: unknown

Type locality: North Sea

The species (Fig. 7) is common in low littoral pools and within the sublittoral zone to -15 m below MLW. The plants usually occur in clumps but single filaments are not infrequent, particularly in estuarine locations. The cells are 350-750  $\mu\text{m}$  (less than 1000  $\mu\text{m}$ ) diameter. The filaments are attached by a single discoid basal cell, which is attenuated and 8-14 times longer than broad. The LWRs of the cells just above the holdfast cell are 4-8 (Fig. 8), decreasing to 1.0-2.0 in the upper portions of the filament (Fig. 9). The species is believed to have an isomorphic alternation of generations, although gametic fusion has not been verified (Kornmann, 1972; Patel, 1972).

#### Distribution and Ecology

*Chaetomorpha melagonium* is a northern species ranging from Long Island Sound to Labrador on the Atlantic coast of North America, and from Oregon to Alaska on the west coast. It occurs primarily in open coastal habitats but scattered estuarine records are known from areas with salinities greater than 20 ppt. The species is found throughout the year. Patel (1972) records zoospore produc-





Figures 7-9. *Chaetomorpha melagonium*. Fig. 7, habit of *C. melagonium*. Fig. 8, basal region of filament with holdfast cell. Fig. 9, upper portion of filament showing the decrease in cell LWR (Scale Fig. 8 and 9 = 50  $\mu$ m).



tion in February. He also observed gamete production but no fusion. Kornmann (1972) recorded bi- and quadriflagellated zoospores in culture but he did not summarize a reproductive phenology.

#### Representative specimens:

**Canada.** NEWFOUNDLAND: Biscay Bay, *Hill 5247* (NFLD), *Hooper 6105* (NFLD). Placentia Bay, *Hooper, Roberge & Reddin 12279* (NFLD). LABRADOR: N. Green Island, *Hooper 8557* (NFLD). NOVA SCOTIA: Tenenee Cove, *Hooper & Wittick 13700* (NFLD). QUEBEC: Cacouma Co., *Cardinal s.n.*, 22 June 1971 (NFLD).

**United States.** ALASKA: Commander Islands, *Stejnegeria 1889* (FH). Juneau, *Saunders 243* (FH). MAINE: Hancock Co., Gouldsboro Bay, *Taylor s.n.*, 18 August 1960 (FH). Mt. Desert, *Holden s.n.*, 12 August 1889 (FH). MASSACHUSETTS: Essex Co., Magnolia, *Clarke s.n.*, 25 October 1889 (FH). Nanhunt, *Young 1884* (FH). NEW HAMPSHIRE: Rockingham Co., Fort Stark, *Mathieson s.n.*, 20 June 1966 (NHA). Dover, *Mathieson s.n.*, 3 October 1977 (NHA). Isle of Shoals, *Lamb A-99* (FH). Rye Ledge, *Newhouse s.n.*, 20 October 1951 (NHA).

#### Taxonomic History

*Conferva melagonium* was described by Weber and Mohr (1804) and transferred to the genus *Chaetomorpha* by Kützing (1849). There has been relatively little confusion regarding this species since that time. *Chaetomorpha picquotiana* had been regarded as a form of this species but has been shown to be a separate entity (see taxonomic history of *Chaetomorpha picquotiana*, p. 183)

#### **Chaetomorpha brachygona** Harvey. 1857 Ner. Bor.-Amer. P. 88

TYPE: *Chaetomorpha brachygona* Harvey. 1857. Ner. Bor. Amer. p. 88, t. 46.

Type locality: Key West, Florida

*Chaetomorpha tortuosa* Maze and Schramm. 1870-77. de Classif. des. alg. dela Guadeloupe. XIX

*Rhizoclonium capillarae* Vickers. 1905. List des Alg. Mar. del la Barbade. Ann. Sci. Nat. Bot. IX: 45-66.

The morphology and habit of this species are similar to that of *Chaetomorpha linum*, with the exception of its narrower dimensions. The entangled filaments of *C. brachygona* have cell diameters of 80-150  $\mu\text{m}$  and LWRs of 1 to 3 (less than 4; Fig. 10). The plant reproduces by vegetative reproduction (i.e., fragmentation) and an isomorphic alternation of generations is assumed.

#### Distribution and Ecology



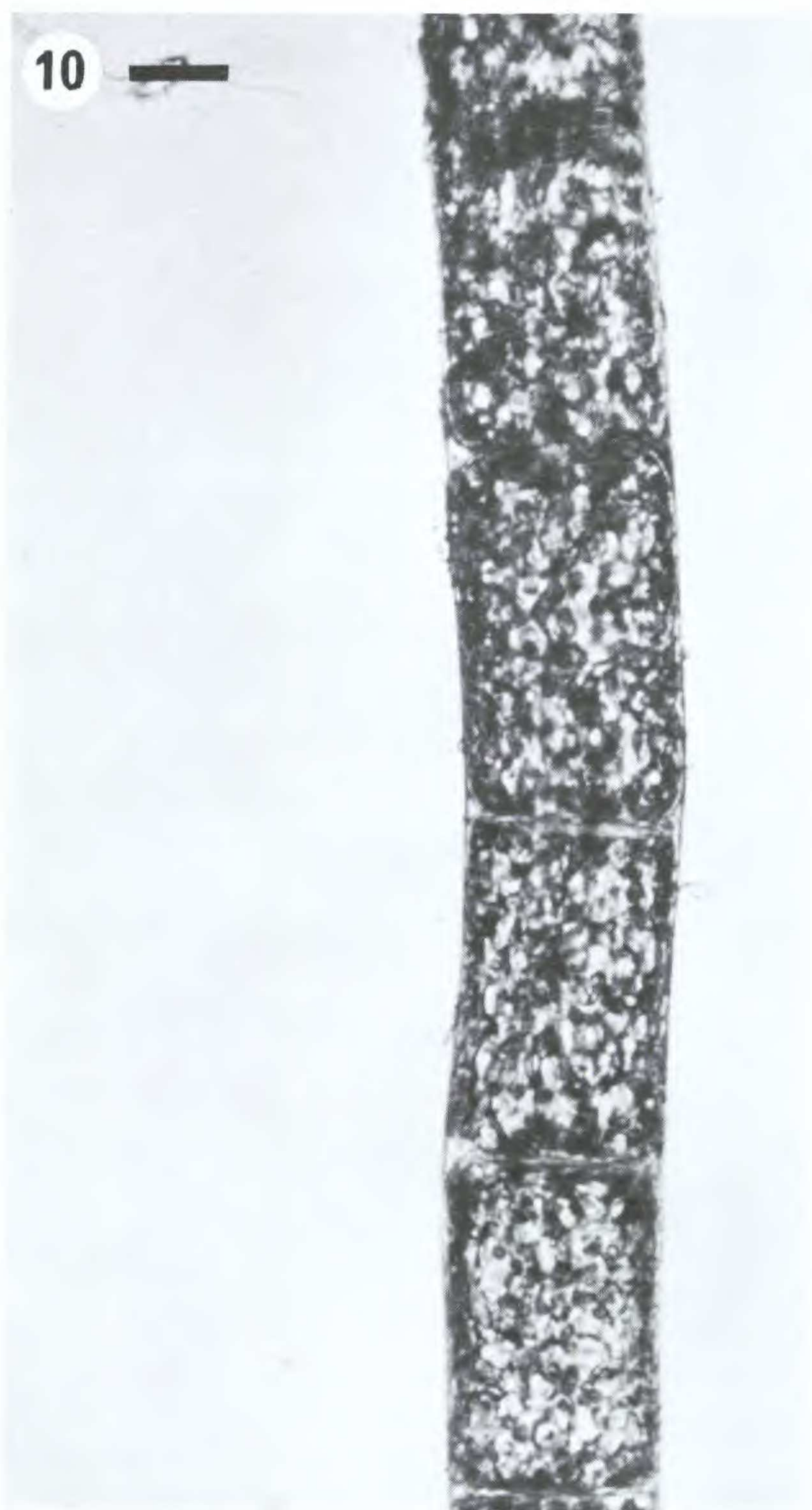


Figure 10. *Chaetomorpha brachygona* (Scale = 50  $\mu$ m).



The plant seems to have the same latitudinal distribution as *Chaetomorpha linum*. Previously *C. brachygona* was recorded only from North Carolina and the tropics. Its previous confusion with *C. cannabina* and *C. capillaris* has probably restricted its delineation in northern latitudes (see taxonomic history). The species occurs in coastal as well as a variety of estuarine habitats if adequate substratum is available.

#### Representative specimens:

**Bermuda.** Hamilton Island, *Harvey s.n.* (FH). St. George's Island, *Lamb & Fralick A-401* (FH). **Canada.** BRITISH COLUMBIA: *Troct & Grant s.n.*, 17 April 1975 (NFLD). NEWFOUNDLAND: Bonavista Bay, *Kells, Hill 4194* (NFLD); 4273 (NFLD). **France.** Albères, *Straus s.n.*, August (NHA). Cannes, *Wit., Nord., Lager Algae Exsicc. 1435* (UC). **Great Britain.** British Isles, *Dixon 11* (FH). **India.** Orientalis, *Børgesen 5310* (UC). **Italy.** Naples, *Reed s.n.*, 9 March 1911 (UC). **Jamaica.** *Manchoinial s.n.* (FH). **Japan.** Okanuma, *Algae Japonicae Exsicc. 93* (FH). **Jugoslavia.** Trieste: *Adriaticae Exsicc. 37* (FH). **New Zealand.** Bay of Islands, *Nash & Nash 3469* (NFLD). **Philippines.** Montalben, *Merril 5096* (FH). **Samoa.** Tutulia Islands, *Setchell 1029* (UC). **Tahiti.** South Peninsula, *Bartlett 17962* (FH). Society Islands, *Setchell & Parks 5182* (UC).

**United States.** ALASKA: New Merlakahtla, *Saunders 46* (UC), 417 (UC). HAWAII: Molakai, *Reed 314* (UC). MAINE: York Co., Kittery, *Mathieson s.n.*, 12 October 1977 (NHA). Bar Harbor, *Leary s.n.*, 15 May 1971 (NHA). NEW HAMPSHIRE: Rockingham Co., Newington, *Mathieson s.n.*, 18 July 1975 (NHA). Newcastle, *Mathieson s.n.*, 23 July 1966 (NHA). WASHINGTON: San Juan Island, *Zeller 1298* (UC). **Australia.** North Queensland: *May NSW 126964* (NFLD).

#### Taxonomic History

The species was first described by Harvey (1857). No dimensional characteristics were given other than that the cells were "as much as, or much shorter than their diameter", and that this species was a more "robust" plant than *Rhizoclonium tortuosum*. The accompanying illustration (Harvey, 1957; Pl. XLVI-A) had no scale, and in comparison, was not noticeably larger than the diameter illustrated for *Rhizoclonium tortuosum* (Harvey, 1857; Pl. XLVI-B). The dimensional characteristics later applied to this species varied somewhat but were in general agreement. The recorded distribution of this species appears to have been restricted due its misidentification as *Chaetomorpha capillare* (Küt.) Børg. (= *Rhizoclonium tortuosum* (Dillw.) Küt.), and *Chaetomorpha cannabina* (Aresch.) Kjellm. (Table 1) owing to variations in measurement attributed to these last 2 species. The variation is partially a reflection of misidentification distributed in exsiccatae. For example, specimen #1435 in Alg. Ag. Dulc. Exsicc. as *Rhizoclonium capillare* and #135



Table 1. Dimensions of *Chaetomorpha cannabina* given in literature

AUTHOR	WIDTH	LENGTH
Areschoug 1843	1/32'''–1/25''' (66 $\mu$ m–84 $\mu$ m)	2–4 times longer than broad
Areschoug 1850	0.1–0.2mm	3–4 times longer than broad
Kützing 1849 (as <i>Cladophora cannabina</i> )	1/35'''–1/15''' (60–40 $\mu$ m)	3–5 times longer than broad
Collins 1909	75–100 $\mu$ m	3–8 times longer than broad (500–600 $\mu$ m)
Setchell & Gardner 1920	45–150 $\mu$ m	3–8 times longer than broad (500–600 $\mu$ m)
Scagel 1966	75–100 $\mu$ m	3–8 times longer than broad (200–450 $\mu$ m)
Taylor 1957	75–100 $\mu$ m	3–8 times longer than broad (500–600 $\mu$ m)
Edelstein & McLachlan 1967	50–60 $\mu$ m	7 diameters

in Alg. Scand. Exisc. fasc. II as *Chaetomorpha cannabina* should properly be identified as *Chaetomorpha brachygona*. For further discussion of the taxonomy of *Chaetomorpha capillare* (Kütz.) Børg. see the taxonomic history of *Rhizoclonium tortuosum* (p. 201).

**Chaetomorpha minima** Collins and Hervey. 1917. The Algae of Bermuda. Pro. Amer. Acad. Arts and Sci. Vol. 53.

TYPE: *Chaetomorpha minima* Collins and Hervey. Herb. Collins.

Filaments attached by a basal cell, erect to approximately 10 mm (Fig. 11), cells cylindrical, 24 to 40  $\mu$ m diameter, 2 to 4 times as long as broad, and occasionally constricted at the end walls.



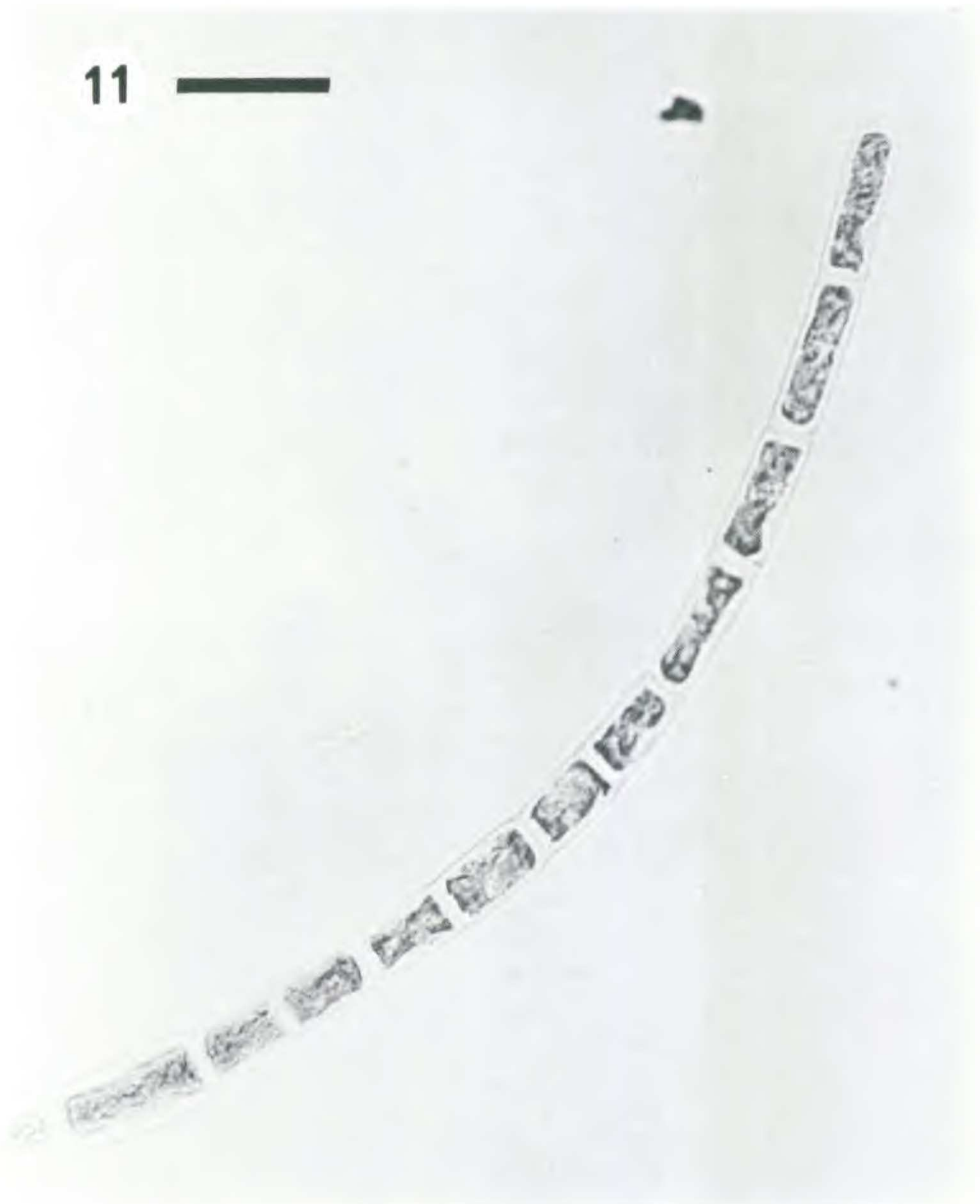


Figure 11. *Chaetomorpha minima* (Scale = 50  $\mu$ m).

#### Distribution and Ecology

The plant was found as an epiphyte on *Chaetomorpha aerea* and *C. melagonium* during the summer and fall of 1977. Previously it was recorded only from the tropics (Taylor, 1960). The New England records of *C. minima* dramatically extend the known distributional limits of the species. Further investigations should demonstrate whether it has a continuous or scattered (disjunct) distribution.



## Representative specimens:

United States. MAINE: York Co., Kittery, *Mathieson s.n.*, 12 October 1977 (NHA); *Hehre s.n.*, 19 November 1976 (NHA).

## Taxonomic History

The species was described from tropical water, as a fine (10–20  $\mu\text{m}$ ), short (<5mm) filament. The author has some reservations regarding the proper designation of this plant. The dimensions of the New England filaments represent an extension beyond the measurements of the type material. The only other species with which the New England material could compare is the Pacific *Chaetomorpha californica* Collins. However, differences lead to exclusion of this species as being equivalent to the New England material. *Chaetomorpha californica* is stated as having a basal cell to 200  $\mu\text{m}$  (noticeably elongate) and constricted at the base. Further, the filaments may attain a length of 20 cm. The basal cell of the New England material is neither noticeably elongate nor constricted at the base. The greatest length of a filament seen in the New England material was 10 mm. Considering the well documented cell size variability of the unbranched species of Cladophoraceae it is considered that the placement of *C. minima* on the New England material is correct.

It should be noted that *C. minima* falls within the dimensional range of *Rhizoclonium riparium* and just outside that of *R. tortuosum*. Reports of Perrot (1965) and Neinhuis (1975) concerning the attached phases of the above species suggest the possibility of *Chaetomorpha minima* representing an attached form of a *Rhizoclonium* species. However, further investigation of the species will be needed to clarify any possible relationships.

## RHIZOCLONIUM

**Rhizoclonium** Kützing. 1843. *Phyco. Gen.* p. 261.

Lectotype: *Rhizoclonium jurgensii* (Mert.) Kütz. *Jurgens Alg. ag.* 1816–22. Decas II #6 (L). (Koster, 1955)

Type locality: North Sea.

The genus *Rhizoclonium* contains species of unbranched, uniseriate filaments. The cells are uni- to multinucleate with a single parietal reticulate chloroplast, which often fragments with age. Few to many pyrenoids are present depending upon the age and size of



the cells. The filaments can occasionally be attached by a basal cell. The LWRs of the cells are 1 to 4 (less than 6). The filaments adhere to coarse algae and other substrates by rhizoidal projections. Filaments tend to show a greater number of proliferations on soft substrata than on hard substrata (Nienhuis, 1975). Reproduction is by fragmentation and by an isomorphic alternation of generations with iso- or anisogamous biflagellate gametes and quadriflagellate zoospores as well possible recycling of their sporophytic stage with bi- or quadriflagellate zoospores (Patel, 1971a).

KEY TO THE NEW ENGLAND SPECIES OF *RHIZOCLONIUM*

1. Filaments entangled with few to many rhizoidal proliferations, 8 to 48  $\mu\text{m}$  diam., from marsh areas and high littoral pools, reproduction by isogamous gametes . . . *R. riparium* p. 203.
1. Filaments entangled in coarse algae in the mid-low littoral zone and sublittoral zones, few or no single celled rhizoidal proliferations; cells 30 to 75  $\mu\text{m}$  diam., reproduction by anisogamous gametes. . . . . *R. tortuosum* p. 198.

**Rhizoclonium tortuosum** (Dillwyn) Kützing. 1845. *Phyco. Germ.* p. 203

Basionym: *Conferva tortuosa* Dillwyn. 1806. *Brit. Conf. Fasc.*

Type: Not in existence (Chapman, 1939)

Type locality: Swansea, England

*Chaetomorpha capillaris* (Kützing) Børgesen. 1925. *Mar. alg. of Canary Is.* p. 45.

*Chaetomorpha tortuosa* Kützing. 1849. *Sps. Alg.* p. 376.

*Rhizoclonium capillariae* Kützing. 1847. *Bot. Zietg.* p. 166.

*Conferva tortuosa* C. Agardh. 1824. *Sys. Alg.* p. 98.

*Conferva tortuosa* J. Agardh. 1842. *Alg. Mar. Med. et Adri.* p. 12.

*Rhizoclonium riparium* (Roth) Harvey f. *validum* Folsie 1878-88. *Witt. & Nord. Alg. ag. Duc. exiscc.* #624.

*Lola implexa* (Harvey) Perrot 1965. *C.R. Acad. Sci. Paris Group 11.* **261**: 503-506.

*Chaetomorpha tortuosa* (Dillw.) Kleen. 1847. *Om Nordlanders Hogra Hafsalger.* p. 45.

The species is a common inhabitant of the low littoral and upper sublittoral zones where it grows in clumps in tide pools, entangled among coarse algae or as "wooly" skeins across bare rocks. The filaments are tortuous and densely entangled, with cell diameters of



24 to 75  $\mu\text{m}$ . The LWRs of the cells are usually 2 to 3 but they may be 1 to 4 (Fig. 12). Rhizoidal proliferations are rare in New England material, and if found they are single-celled. The species has an isomorphic alternation of generations with anisogamous gametes (Fig. 13) and quadriflagellate zoospores (Hamel, 1929).

#### Distribution and Ecology

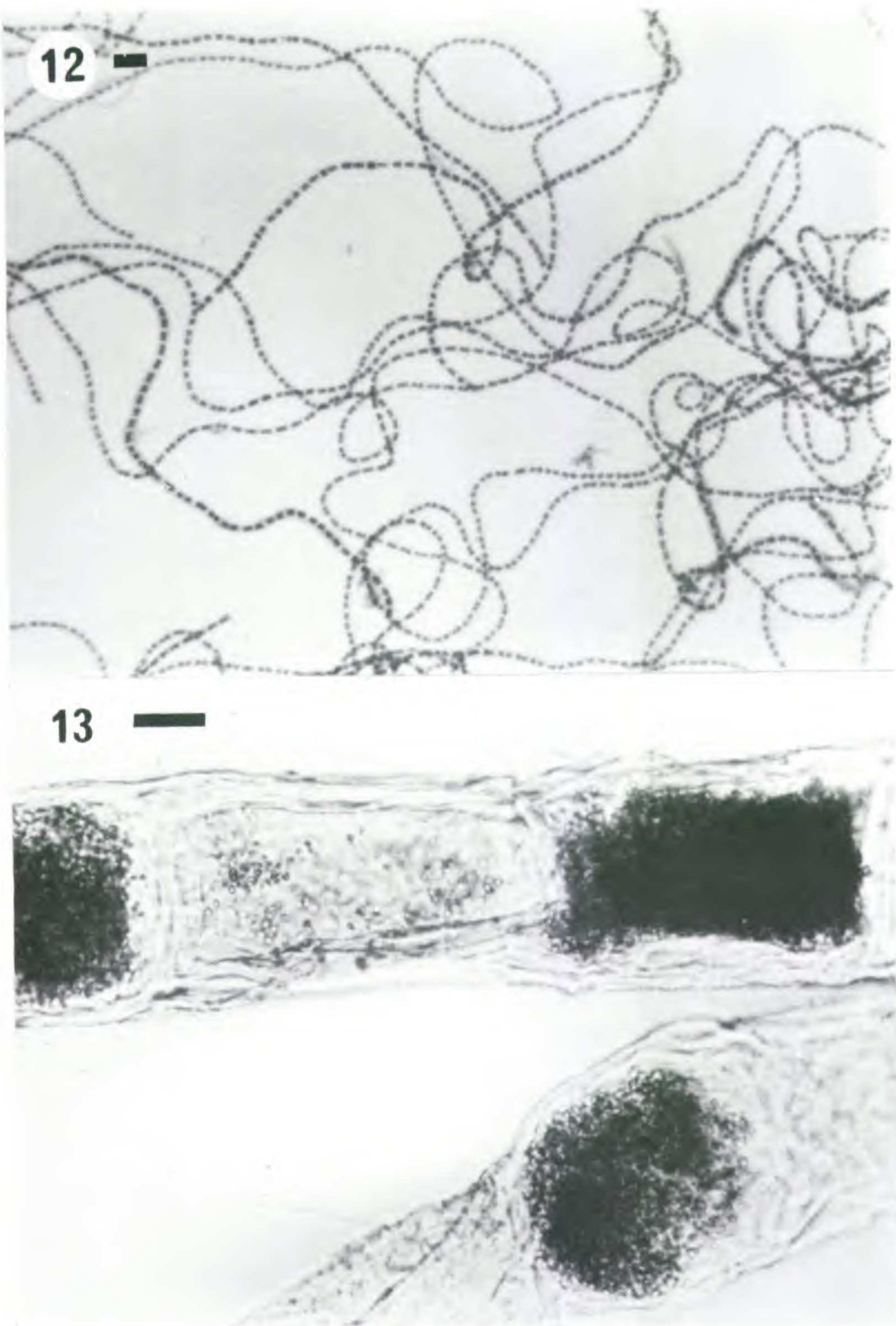
*Rhizoclonium tortuosum* shows a broad geographical distribution extending from Florida to Labrador, and Southern California to Alaska on the coasts of the United States, and from France, Norway, the Philippines, and Formosa. In New England, it is most common in the littoral region on the open coast but it survives in estuarine habitats where the salinities approximate 15 ppt.

#### Representative specimens:

**Azores.** San Miguel, *Canneiro* 755 (UC). **Bermuda.** Paget Island, *Bernatowicz* 51-764 (UC). **Canada.** BRITISH COLUMBIA: Felix Bay, *Root & Grant* s.n., 17 April 1975 (NFLD). NEWFOUNDLAND: Allan's Lighthouse, *Hooper* 7401 (NFLD). Bonne Bay, *Hooper & Gibbons* 11197 (NFLD); Conception Bay, *Hill* 3321 (NFLD); Gros Morne Park, *Hooper, Gibbons & Roberge* 11710 (NFLD). NOVA SCOTIA: Annapolis Co., Tammy's Beach, *Parsons* 6 (NFLD). QUEBEC: *Cardinal* s.n., 11 August 1971 (NFLD). **Canary Islands.** Las Almas, *Børghesen* 3916 (UC). **France.** Algeres, *Hauk et Richter* Phyco. Univer. 728 (UC). **Formosa.** Diabouratsu, *Yamada* 272789 (UC). **Netherlands East Indies.** Pali, *Yong Seh* B282 (UC). **Norway.** Novegia, Christionsand, Ekman in Alg. Scand. Exsicc. Ser. Fasc. Primus 29 (UC). **Philippines.** Luzon, *Merrill* 7456 (UC); Camiguin Island, *Setchell & Parks* 5160 (UC).

**United States.** ALASKA: Tutkutat Bay, *Saunders* 192 (UC); Kodiak, *Setchell & Lawson* 5141 (UC); Orca, *Setchell & Lawson* 5269 (UC). CALIFORNIA: Los Angeles Co., Long Beach, *McClatchie* 1171 (UC); Point Lobos, *Gardner* 3396 (UC); Monterey Co., Carmel River, *Doty* 5868 (UC); San Mateo Co., Moss Beach, *Doty* 6055 (UC). FLORIDA: Monroe Co., Key West, *Hitchcock* s.n., (NHA). HAWAII: Keaukaha, *Setchell & Setchell* 10133 (UC). MAINE: Cumberland Co., Reid State Park, *Britt* s.n., 15 July 1967 (NHA); Washington Co., W. Quoddy Head, *Searles* 215D (NHA); York Co., Eliot, *Searles* s.n., 2 July 1966 (NHA); Kittery, *Blair* s.n., 20 December 1977 (NHA); Isle of Shoals, *Blair* s.n., 16 April 1976 (NHA). MASSACHUSETTS: Barnstable Co., Woods Hole, *Newhouse* s.n., 14 July 1951 (NHA); Essex Co., Salem, *Femino* s.n., 22 July 1966 (NHA); Cape Ann, *Searles* s.n., 2 May 1966 (NHA). Nanhaunt, Collins Phyco. Univ. 627E (UC). NEW HAMPSHIRE: Rockingham Co., Isles of Shoals, *Conway & Shipman* s.n., 22 July 1966 (NHA); Newcastle, *Tveter* s.n., 20 October 1973 (NHA); Rye, *Hehre & Conway* s.n., 8 January 1966 (NHA); Strafford Co., Durham, *Mathieson* s.n., 11 August 1977 (NHA). Dover, *Conway & Shipman* s.n., 16 August 1966 (NHA). NEW YORK: Putnam Co., Cold Spring Harbor, *Broon* s.n., 23 July 1908 (UC). OREGON: Coos Co., Sunset Bay, *Phinney & Hanson* 282 (UC); North Bay, *Hanson* s.n., 289 (UC). RHODE ISLAND: Newport Co., Cloud Point, *Setchell* s.n., 17 June 1923 (UC). WASHINGTON: Clallam Co., Friday Harbor, *Gardner* 4083 (UC); San Juan Is., *Setchell & Gardner* 219 (UC).





Figures 12 and 13. *Rhizoclonium tortuosum*. Fig. 12, habit of filaments (Scale = 150  $\mu$ m). Fig. 13, reproductive cell with anisogametes (Scale = 10  $\mu$ m).



### Taxonomic History

The species was originally described by Dillwyn (1806) as *Conferva tortuosa*. No dimensional characters are given in the description, other than the statement that "the filaments are fine as hair of the human head", and that the cells are nearly twice as long as broad. A type specimen was not designated and the published drawing shows no scale. Chapman (1939) was unable to find a type specimen but succeeded in finding a specimen identified by Dillwyn as *Conferva tortuosa*. The filaments were 34 to 48  $\mu\text{m}$  diam. with a mean of 40  $\mu\text{m}$ , and were 1 to 2 times as long as broad. Kützing (1845) transferred *Conferva tortuosa* Dillwyn to *Rhizoclonium tortuosum*, stating that its diameter was  $1/70'''$  ( $''' = \text{a ligne or } 2116 \mu\text{m}$ ) or 31  $\mu\text{m}$  wide and 1 to 1.5 times as long as broad.

Confusion arose between *Rhizoclonium tortuosum* and Kützing's (1849) *Chaetomorpha tortuosa*. The confusion was examined by Chapman (1939) and will only be reviewed here. To examine this confusion we must look back to the origins of *C. tortuosa* and *Rhizoclonium capillare* (Kützing, 1847). The species *R. capillare* was characterized by cells measuring  $1/45'''$  (47  $\mu\text{m}$ ) and 1 to 2 times longer than broad. Later Kützing (1849) described *Chaetomorpha tortuosa* stating it was characterized by cells  $1/45'''$  to  $1/40'''$  (47 to 57  $\mu\text{m}$ ) in diameter, rigid, curled, tortuous, and 1 to 2 times as long as broad. *Rhizoclonium capillare* Kützing was placed as a synonym of *Chaetomorpha tortuosa*. The basionym cited by Kützing for both *Chaetomorpha tortuosa* and *Rhizoclonium capillare* is *Conferva tortuosa* J. Agardh, which is based on *Conferva tortuosa* C. Agardh (J. Agardh, 1842). *Conferva tortuosa* C. Agardh is in turn based on *Conferva tortuosa* Dillwyn (C. Agardh, 1824). However, *Conferva tortuosa* Dillwyn is the basionym for *Rhizoclonium tortuosum* (Dillwyn) Kützing (1845). Thus, there had been an inadvertent establishment of two species on a single basionym. Therefore, either the two species are united under one name (brought into synonymy), or if two species are separate entities, the invalid name is discarded and the second species is renamed. An examination of the original description for *R. capillare* and *R. tortuosum* indicates that Kützing's original intent was to describe two separate taxa. The cells of *Rhizoclonium tortuosum* were listed as  $1/70'''$  (31  $\mu\text{m}$ ) diameter and 1.5 times longer than broad (Kützing, 1845), while *R. capillare* cells were described as being  $1/45'''$  (47  $\mu\text{m}$ ) diameter and 1 to 2 times



longer than broad (Kützing, 1847). Børgesen (1925) noted Kützing's intent to describe two separate species, and the incorrect basionym declaration. Accordingly, he made the combination *Chaetomorpha capillare* (Kützing) Børgesen citing *R. capillare* as the basionym. The continued confusion as to the proper naming and dimensional characteristics of *C. capillare* is evident in a variety of recent studies (Kornmann & Sahling, 1977; Christensen, 1975; Price, 1967) which cite the taxon as either *C. tortuosa* or *C. capillare*. However, recent work (Blair, 1978) has shown *Chaetomorpha capillare* (Kützing) Børgesen and *Rhizoclonium tortuosum* to be conspecific on the basis of morphological continuity and indistinguishable habit. Thus, *C. capillare* (Kütz.) Børg. and *R. capillare* Kütz. are synonyms of *R. tortuosum* (Dillw.) Kütz.

Foslie (in Wittrock & Norstedt, 1877-1887) described *Rhizoclonium riparium* (Roth) Harvey f. *validum* Foslie stating that the form was wider and had a greater length than *R. riparium*, being 26 to 36  $\mu\text{m}$  wide, 0.25 to 2.33 times longer than broad, and without rhizoids (Koster, 1955). Rosenvinge (1893) elevated the form to varietal status, increased the width range to 30-50  $\mu\text{m}$ , and indicated that rhizoids could be numerous. Some authors (Stockmayer, 1898; Chapman, 1939) have reduced *R. tortuosum* to synonymy under *R. riparium* f. *validum*, while Koster (1955) preferred to synonymize *R. riparium* f. *validum* under *R. tortuosum*, which would be the correct synonymy on the basis of priority of publication. Therefore, *R. riparium* f. *validum* was also placed as a synonym of *R. tortuosum* (Koster, 1955).

Hamel (1929) showed that *Rhizoclonium lubricum* Setchell et Gardner exhibited anisogamous reproduction. The character is unique within the Cladophoraceae and led to the establishment of *Lola* Hamel for unbranched cladophoralean algae with anisogamous reproduction. Perrot (1965) later showed that *Rhizoclonium implexum* Harvey (= *R. tortuosum* (Dillwyn) Kützing; see Chapman, 1939) has anisogamous reproduction. Accordingly he transferred *R. implexum* to *Lola*. Presently the species is referred to as either *Rhizoclonium tortuosum* (Dillwyn) Kützing or *Lola tortuosa* (Dillwyn) Perrot. It should be noted that the establishment of a genus on a single characteristic (i.e., anisogamous reproduction) despite other similarities with the *Rhizoclonium* sp. is tenuous. The use of anisogamous reproduction as a generic character is further



questionable in light of the fact that other green algal genera, (i.e., *Sphaeroplea*, *Chlamydomonas*) contain species that range from isogamous to anisogamous. The present author, therefore, favors the retention of *Rhizoclonium tortuosum* in the genus *Rhizoclonium*.

**Rhizoclonium riparium** (Roth) Harvey. 1846. *Phyco. Brit.* IV p. 1238

Basionym: *Conferva riparia* Roth. 1797. *Catal. Bot. Fasc.* 1.

Type: *Conferva riparia* Roth leg. Mertens. 1803. Norderney, Germany ex Herv. Hooker (K).

Type Locality: Morderney, Germany.

*Rhizoclonium jurgensii* (Mertens) Kützing. 1843. *Phyco. Gen.* p. 261.

*R. lacustre* Kützing 1847. *Diag. Verner. odea Dritis. Alg. Bot. Ziet.*

*R. implexum* (Dillwyn) Kützing. 1845. *Phyco. Germ.* p. 206.

*Conferva implexa* Dillwyn. 1806. *Brit. Conf.* p. 46 t. b.

*Rhizoclonium interruptum* Kützing. 1849. *Sps. Alg.* p. 384; 1853. *Tab. Phyc.* III t. 69, f. 2.

*R. kernerii* Stockmayer. 1898. *Über die Algen.* p. 583.

*R. kochianum* Kützing. 1845. *Phyco. Germ.* p. 206.

The species is found in high tide pools and marshes on the open coast as well as within high marsh communities in estuaries. The filaments are lax and entangled, with a cell diameter of 8 to 45  $\mu\text{m}$  diameter. The LWRs vary between 1 and 4 ( $< 6$ ). Rhizoidal proliferations are sparse to abundant in New England material, and consist of single or multiple cells. The plant has never been found attached (basally) in New England although it shows an attached stage in culture (Neinhuis, 1975). *Rhizoclonium riparium* exhibits an isomorphic alternation of generations with isogamous gametes and bi- and quadriflagellate zoospores (Neinhuis, 1975).

#### Distribution and Ecology

Neinhuis (1975) and Koster (1955) have given extensive summaries of the ecology and distribution of the species. Accordingly only an overview is given and reference is made to the above articles for a variety of details on the plant's distribution and ecology. *Rhizoclonium riparium* has a world-wide distribution, being recorded from the Netherlands, Europe and Japan. It is extremely euryhaline, being found in a broad range of estuarine and coastal habitats. Within the Great Bay estuary system *R. riparium* is usually found entangled among the bases of *Spartina alterniflora* on muddy sub-



strata within the littoral zone, also reaching the headwaters of many riverine tributaries. Some samples of *R. riparium* may reach the dimensions of *R. tortuosum*, from which it may be separated by its broader estuarine distribution and differential reproductive morphology, i.e., isogamous for *R. riparium* and anisogamous for *R. tortuosum*.

#### Representative specimens:

**Canada.** NEW BRUNSWICK: Charlottes Co., Campobello Island, *Hehre & Conway C1911* (NHA); South Wolf, *Conway et al. W-77* (NHA). NEWFOUNDLAND: Bonne Bay, *Hooper & Williams 7977* (NFLD), Bonavista Bay, *Mathieson NF202* (NHA); Conception Bay, *South et al. 4509* (NHA). **Tahiti.** Society Islands, *Setchell & Parks s.n.*, July 1922 (UC), *Hoenneck & Meerlagen 478* (UC).

**United States.** DELAWARE: Lewes, *Mathieson et al. s.n.*, 14 August 1966 (NHA). MAINE: Aroostook Co., Eagle Island, *Collins 2116* (NHA); Hancock Co., Camden, *Hooper 951* (NHA); Washington Co., Lubec, *Hehre 3182* (NHA); York Co., Ogunquit, *Searles s.n.*, 7 April 1966 (NHA); Eliot, *Searles s.n.*, 30 April 1966 (NHA). NEW HAMPSHIRE: Rockingham Co., Greenland, *Mathieson & Hehre s.n.*, 14 September 1966 (NHA), *Hehre et al. s.n.*, 8 July 1966 (NHA); Newington, *Mathieson s.n.*, 9 September 1977 (NHA); Hampton, *Mathieson s.n.*, 11 September 1969 (NHA); Portsmouth, *Croasdale s.n.*, 28 July 1938 (NHA), *Blair s.n.*, 17 August 1977 (NHA); Newcastle, *Mathieson s.n.*, 20 April 1967 (NHA); Strafford Co., Durham, *Mathieson s.n.*, 20 June 1966 (NHA); Dover, *Hehre & Shipman s.n.*, 24 June 1966 (NHA); Durham, *Mathieson s.n.*, 27 July 1977 (NHA); Newington, *Reynolds NB381* (NHA).

#### Taxonomic History

This species was first described by Roth (1793) as *Conferva riparia* based upon its thin, twisted, bifurcating habit ("*apice tantum divisa et pierumque bifia*"). No dimensional characters were given, other than that the width was one half the length, ("*diametro sesquialongioribus*"). In addition, no type specimen nor drawing was indicated. Koster (1955) found a specimen of *Rhizoclonium riparium* collected by Mertens from the type locality of Norderney, Germany. She assumed that it was part of the type collection. The specimen contained a mixture of *Rhizoclonium riparium* (Roth) Harvey and *Caldophora fracta* (Dillwyn) Kützing f. *haukii* (Børgesen) Slootweg. Koster felt the *Cladophora* fraction of this specimen pertained to Roth's description of branching. Harvey (1845-51), when transferring the species from *Conferva* to *Rhizoclonium*, selected only the *R. riparium* element from the mixture (Koster, 1955). Accordingly, Koster proposed that the specimen from Norderney, Germany, in the Kew Herbarium should be designated as a lectotype.



The filaments are 18 to 30  $\mu\text{m}$  wide and cells are 1.5 to 2.5 times longer than broad (Koster, 1955).

Specimens that have been identified as *Rhizoclonium riparium* are commonly found, but the degree of rhizoidal proliferation is variable. As a result a large number of forms and varieties have been described depending upon the presence, absence and morphology of rhizoids. For example, *R. riparium* (Roth) Harvey var. *polyrhizum* (Lyngbye) Rosenvinge is described as having many rhizoids with one to few cells, while *R. riparium* (Roth) Harvey var. *implexum* (Dillwyn) Rosenvinge is recorded to have few or no rhizoids. Koster (1955) proposed the distinction of "*status radicans*" and "*status arrhizum*" for those specimens with a variable occurrence of rhizoids with the belief that rhizoidal proliferations were influenced by environmental factors.

Nienhuis (1975) recorded extreme variability of filament and rhizoidal morphology for *Rhizoclonium riparium* populations in the Netherlands. After extensive field and culture studies, he found that filament diameter and the degree and size of rhizoidal proliferations were influenced by tidal elevations, firmness of substrates, and salinity. The rhizoidal variability he observed encompassed the morphologies recorded for *R. implexum* (Dillwyn) Kützing (Kützing, 1849), *R. hieroglyphicum* (C. Agardh) Kützing (Kützing, 1849) and *R. riparium* (Roth) Harvey. As a result he synonymized *R. implexum* and *R. hieroglyphicum* with *R. riparium* (Roth) Harvey.

#### DISCUSSION

As reflected in the Taxonomic History sections of this paper, a great deal of confusion concerning specific delineation has existed within these genera. While the present report addresses some of the questions that have arisen, many more remain unanswered. For example, difficulties may arise in discerning non-reproductive *Rhizoclonium tortuosum* and *R. riparium* within the region of dimensional overlap (24 to 45  $\mu\text{m}$ ). Habitat information may aid in their determination as *R. tortuosum* is found in the low littoral to upper sublittoral while *R. riparium* is found in areas of extreme environmental fluxes, such as marshes and mudflats. The differential reproductive phenology, however, confirms the need for specific separation of the two species (*Rhizoclonium tortuosum* showing



anisogamous reproduction while *R. riparium* reproduces isogamously).

Within the genus *Chaetomorpha*, questions arose as to the taxonomic validity of *Chaetomorpha cannabina* (Aresch.) Kjell. as no specimens examined (field or herbarium) fit the dimensions cited for the species. In general, the species is considered to vary in diameter from 75 to 100  $\mu\text{m}$  with cell lengths being 3 to 8 diameters (500 to 600  $\mu\text{m}$ ) long (Taylor, 1957). The dimensions credited to this species have varied considerably from author to author (Table 1). Areschoug (1843) described the species *Conferva cannabina*, and distributed specimens of the species in the *Algae Scandinavicae Exisccatae* (1840). Areschoug (1843) referenced a previously published species, *Conferva auricoma* Suhr (Suhr, 1840) stating that through communication with Suhr, it was believed that the two plants were the same. If in fact the two species are the same then the correct designation of the taxon should be *Chaetomorpha auricoma*. However, questions still exist as to the conspecificity of Suhr's *Conferva auricoma* and Areschoug's *Conferva cannabina*. At present, specimens of *C. auricoma* Suhr have not been examined. Specimens of *Conferva cannabina* Areschoug, distributed in *Alg. Scand. Exiscc.* (1840; #14) were examined through the courtesy of the Riksmuseet (s) and Rijksherbarium (L) and represent a remotely branched member of the Cladophoraceae. However, until type material of *Conferva auricoma* Suhr can be examined, the proper generic placement and specific classification of the two species must be reserved. It should be noted that the herbarium specimens examined from various institutions identified as *Chaetomorpha cannabina* were referable to either *Chaetomorpha brachygona* or *Rhizoclonium tortuosum*, and none fit the description attributed to *C. cannabina*. Concern about possible conspecific relationships existing between some of the more narrow *Chaetomorpha* and *Rhizoclonium* species have previously been noted (p. 197).

Finally, with regard to the separation of the genera *Chaetomorpha* and *Rhizoclonium*, a review of the characters used to separate the two genera shows none of the characters to be valid criteria. The names *Rhizoclonium* and *Chaetomorpha* bring forth specific thoughts of shape and form for many taxonomists. However, the characters that have been used to separate the genera have been shown to be erroneous criteria or based on environmentally



variable characteristics. The genus *Rhizoclonium* was originally described with a single sentence "*Trichomata parenchymatica, coelogonimica, ramus verticales, radicoutes emittentis*" (Kützing, 1843). The description of *Chaetomorpha* (Kützing, 1845) was not much more elaborate but did point out the unbranched nature of the plant, and that it was a uniseriate filament with laminated cells that were as long as broad or longer, but less than 4 times the width.

Previous authors have employed various characters to differentiate the genera: cell shape (Collins, 1909; Setchell & Gardner, 1920), mode of attachment (Bold & Wynne, 1978; Abbott & Hollenberg, 1976; Taylor, 1957; Setchell & Gardner, 1920; Collins, 1909), and number of nuclei per cell (Setchell & Gardner, 1920). The most common criterion for separation of the genera has been mode of attachment, with basal holdfasts in *Chaetomorpha* and rhizoids in *Rhizoclonium*. However, past studies have shown *Rhizoclonium* species to have basal holdfast stages at some point in their life history (*R. tortuosum*: Perrot, 1965; *R. riparium* (= *R. implexum*) (Dillw.) Küt. : Nienhuis, 1975). The presence or absence of rhizoids has also been used as a diagnostic character for delineation of *Rhizoclonium*. Nienhuis (1975) and Patel (1971b) have shown rhizoidal proliferation and complexity to be affected by light intensity, substratum firmness, light quality, and temperature. The demonstrated variability of this character, and the fact that the New England populations of *R. tortuosum* often lack rhizoids, makes this character of little use in generic separation.

Chapman (1939) cited the width of the filament as the distinguishing character between the species. The original description of the genera, however, gave no dimensional characteristics. Further, a continuum of cell widths is present between *Chaetomorpha* and *Rhizoclonium* (Table 2). Other criteria, such as pyrenoid number and number of nuclei per cell, have been shown to vary with the cell volume and are not specific or generic indicators in the unbranched Cladophoraceae (Prasad, et al., 1973; Price, 1967; Carter, 1919).

It appears then, that the question must be raised as to the continued separation of the two genera, at least on the basis of traditional characteristics. Further information reflecting the close relationship between these two groups can be seen in the chromosome numbers of the species within the genera (Table 3). As stated by Sinha (1953), there appears to be a polyploid series with a base



Table 2. Cellular dimensions of representative species of *Chaetomorpha* and *Rhizoclonium*

SPECIES	CELL WIDTH	CELL LENGTH
<i>Rhizoclonium riparium</i> (Nienhuis, 1975)	8 to 48 $\mu\text{m}$	1 to 4 times the width
<i>Chaetomorpha minima</i> (Taylor, 1960 & present study)	10 to 40 $\mu\text{m}$	1 to 2 times the width
<i>R. tortuosum</i> (= <i>Lola tortuosa</i> ) (present study)	27 to 75 $\mu\text{m}$	2 to 3 (1-4) times the width
<i>Chaetomorpha brachygona</i> (present study)	75 to 150 $\mu\text{m}$	1 to 2 times the width
<i>C. linum</i> (present study)	150 to 450 $\mu\text{m}$	0.75 to 1.5 times the width

Table 3. Chromosome numbers of various *Chaetomorpha* and *Rhizoclonium* species

SPECIES	$2n$	$1n$	AUTHOR
<i>Rhizoclonium riparium</i>	36	18	Sinha (1958)
<i>R. tortuosum</i>	24	—	Sinha (1958)
	22	—	Patel (1971b)
	20	10	Perrot (1965)
<i>Chaetomorpha linum</i>	36	18	Patel (1971a)
	36	18	Sinha (1958)
<i>C. aerea</i>	24	12	Patel (1971a)
	20	10	Hartman (1929)
<i>C. melagonium</i>	24	12	Patel (1972)

number of 6. Although enough information is available at present to question the validity of generic separation, additional information concerning the remaining species of *Chaetomorpha* and *Rhizoclonium* must be collected before the final disposition of the two genera is made.



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